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TAXONOMIC NOTES ON *VERBENA BONARIENSIS* (VERBENACEAE) AND RELATED SPECIES IN THE USA

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ABSTRACT

Verbena bonariensis, as previously recognized in the USA, is here recognized to include two distinct species, both native to South America and both widespread in geographic range. *Verbena incompta* is the more common of the two and is characterized by relatively smaller flowers and eglandular vestiture; *V. bonariensis* sensu stricto has larger, showy flowers and glandular stems, peduncles, and calyces. *Verbena litoralis* has sometimes been recognized to occur in the USA, but such records have proved to be *V. brasiliensis* and *V. montevidensis*. *Verbena litoralis* sensu stricto is native to northwestern South America, Central America, and Mexico, apparently not reaching the USA even as an adventive. *Verbena montevidensis* is documented to be naturalized in Alabama, Arkansas, Florida, Georgia, Louisiana, Oregon, and Texas. Each of these species is distinctive in North America.

KEY WORDS: *Verbena bonariensis*, *V. incompta*, *V. brasiliensis*, *V. litoralis*, *V. montevidensis*, Verbenaceae, taxonomy, USA

Recent studies of *Verbena bonariensis* L. and *V. brasiliensis* Vell. and close relatives (Yeo 1990; Michael 1995, 1997, 2008; Munir 2002; O'Leary et al. 2007) have disagreed in typification and concepts of morphological definition and taxonomic rank. These taxa are native to South America but have become widely naturalized worldwide in tropical and subtropical regions. They have been studied in preparation of a taxonomic treatment of *Verbenaceae* for the developing Flora of North America series, and the results are reported here at a greater level of detail than will be included in the FNA comments. Of the taxa considered, Perry (1933) recorded the presence of *V. bonariensis*, *V. brasiliensis*, and *V. litoralis* Kunth in the USA; *V. montevidensis* Spreng. has since been recognized to occur here; and the occurrence in the USA of a species recently segregated from *V. bonariensis* is unequivocally documented here for the first time. The recent overview by Sanders (2001) included comments on *V. bonariensis*, *V. brasiliensis*, *V. litoralis* and *V. montevidensis*.

Detailed typification has been provided in studies cited above. Some of that is repeated or restudied here for ease of reference in documentation of present interpretation and because some of the names in synonymy may be involved in future arrangements to portray the taxonomy, especially with reference to *V. litoralis* and its closest relatives. Also, disagreements exist between the present study and previous ones.

Variation in *Verbena bonariensis* sensu lato and the status of *V. incompta*

Yeo (1990) observed that among plants generally identified as *Verbena bonariensis*, which is characterized by clasping leaf bases, some are more similar to *V. brasiliensis* (which has tapering leaf bases) in a suite other features, and he accommodated these latter plants by broadening the concept of *V. brasiliensis* to include plants with clasping bases. Shortly afterward, the *V. brasiliensis*-like plants (fide Yeo) with clasping leaf bases were formally described as *Verbena incompta* P.W. Michael

(Michael 1995), in recognition of their apparent evolutionary independence from both *V. bonariensis* and *V. brasiliensis*. The type of *V. incompta* is from Australia, where it is naturalized, but native to South America. Munir (2002) and O'Leary et al. (2007), in contrast, because of a different interpretation of the Linnaean type of *V. bonariensis*, considered *V. incompta* as synonymous with typical *V. bonariensis* and recognized the variants as *V. bonariensis* var. *conglomerata*. Munir and O'Leary et al. both characterized var. *conglomerata* as essentially the same in morphology as Michael's *V. incompta*. Var. *conglomerata* was treated by Michael, followed here, as a synonym of typical *V. bonariensis*.

Recognition of two entities within what previously was considered as *Verbena bonariensis* sensu lato is confirmed in the present study. Munir mapped var. *conglomerata* as sympatric in Australia with var. *bonariensis*, nearly identical in range, and observed that they are "easily separated"—especially by spike shape and corolla tube length. He did not note the occurrence of hybridization or integradation between the two. O'Leary et al. noted that although var. *conglomerata* is more restricted in native geographic range, it is sympatric in South America with typical *V. bonariensis*. The morphological description of var. *conglomerata* by O'Leary et al. was similar to Munir's—and apparently as with Munir, treatment of the two entities as conspecific varieties was based on the observation that their distinctions did not meet a criterion, unspecified, for recognition at specific rank ("Las differencias entre las dos variedades de *Verbena bonariensis* … lo cual no justifican la separación de este taxon a nivel específico.").

Distinctions, as recognized and emphasized in the previous studies, between the two entities of *Verbena bonariensis* sensu lato are these. Diagnostic features observed in the present study are contrasted in the key further below.

Michael (1995, 2008)

a. Corollas prominently exserted from calyces, tubes 3.5–5 mm; peduncles and calyces stipitate-glandular; anthers inserted near middle of corolla tube; floral bracts shorter than calyces; mature nutlets 1.5–2.1 mm ..... **Verbena bonariensis**

a. Corollas only slightly exserted from calyces, tubes 2.5–3.5 mm; peduncles and calyces usually eglandular; anthers inserted in distal third of corolla tube; floral bracts longer than calyces; mature nutlets 1.2–1.5 mm ..... **Verbena incompta**

Munir (2002)

a. Spikes contracted into capitate or subcapitate clusters; corolla tube much protruding, ca. 1.5–2 times longer than the calyx; peduncles glandular ..... **Verbena bonariensis** var. **conglomerata**

a. Spikes subcylindric, aggregate but not in capitate or subcapitate clusters; corolla tube slightly exserted, mostly less than 2 times longer than the calyx; peduncles eglandular **Verbena bonariensis** var. **bonariensis**

O'Leary et al. (2007)

a. Corolla tubes generally more than 5 mm, nearly twice as long as the calyx; floral bracts with obtuse or subobuse apices, generally shorter than the calyx; peduncles glandular; leaf blades generally narrowly elliptic to sublinear ..... **Verbena bonariensis** var. **conglomerata**

a. Corolla tubes rarely more than 5 mm; floral bracts with acute apices, equalling the calyx or longer; peduncles eglandular; leaf blades ovate-elliptic ..... **Verbena bonariensis** var. **bonariensis**

The present study documents the existence of both entities in the USA and concludes that their broad sympatry without intermediacy is evidence for reproductive isolation. Each is recognized here at specific rank. The interpretation of the identity of the type of *Verbena bonariensis* also is in agreement with Michael (1995, 2008) and the two appropriate names are *V. bonariensis* and *V. incompta*.

VERBENA BONARIENSIS L., Sp. Pl. 1: 20. 1753. **TYPE**: **[Argentina]**. "Habitat in agro Bonariensi" (this referred to the origin of the plant illustrated by Dillenius rather than the collection locality of the Linnaean type, as noted by Yeo, fide C. Jarvis). **LECTOTYPE** (Moldenke 1962a, p. 252, fide Jarvis 2007): Herb. Linn. No. 35.11 (LINN, digital image!). Michael (1995, 2008) reckoned that Yeo's lectotypification (1990) was to be preferred, but Jarvis chose the earlier one of Moldenke. In any case, both Yeo and Moldenke indicated that 35.11 should be the lectotype. Narrow leaves and long corolla tubes are evident in the digital image, placing the identity in agreement with observations of Yeo and Michael. Yeo studied the type material in London (BM and LINN) and his application of the name is unambiguous.

Verbena bonariensis var. *conglomerata* Briq., Ark. Bot. Stockh. 2: 10, t. 3b. 1904. **LECTOTYPE** (Munir 2002, p. 36): **Brazil**. Rio Grande do Sul: Porto Alegre, in pascuis siccis arenosis, 12 Oct 1892, *C.A.M. Lindman A.473* (S digital image!; isolectotypes: S digital image!).

Verbena intercedens Briq., Bull. Herb. Boissier, ser. 2(4): 1057. 1904. **LECTOTYPE** (O'Leary 2006, p. 496): **Paraguay**. Caraguatay, in campis humidis, 1898-1889, *E. Hassler 3324* (G; isotypes: G, K fide O'Leary). Syntype: Paraguay, *Hassler 6149* (B photo-MO!, MO!). The illustration of *V. intercedens* in O'Leary et al. (2007, Fig. 5) is an excellent portrayal of the species identified here as *V. bonariensis* L.; the accompanying description characterizes the floral bracts as "hispidas con pelos glandulares."

Verbena inamoena Briq. Bull. Herb. Boissier, ser. 2(4): 1058. 1904. TYPE: **Paraguay**. Tobaty, Aug 1899, *E. Hassler 3164* (holotype: G, isotype: SI). Not seen; synonym of *V. bonariensis* var. *conglomerata* fide O'Leary et al. (2007).

Verbena bonariensis var. *hispida* Moldenke, Phytologia 33: 374. 1976. TYPE: **Brasil**. Rio Grande do Sul: Villa Germanica, Mar 1906, *A. Bornmüller 647* (holotype: MO!; isotype: M). Not seen; synonym of *V. intercedens* fide O'Leary et al. (2007).

Plants annual, taprooted or with ligneous fibrous roots. **Stems** erect, 80–150 cm, hirsute to hirsutulous, densely so distally, sparsely to densely stipitate-glandular. **Leaves** persistent, basal and midstem oblong-lanceolate to oblong-oblanceolate, basally clasping and auriculate, 5–11 cm x 10–20 mm, distal (above midstem) becoming linear-lanceolate to linear-oblanceolate, veins impressed adaxially, both surfaces hirsutulous to hirsute-hirsutulous or hirtellous, usually sparsely to densely stipitate-glandular, margins sharply serrate, narrowly revolute; petioles absent. **Spikes** in 3s, forming compound cymes, the central mostly sessile on peduncles 0(–4) mm, inflorescence aspect corymbiform, comprising relatively compact and distinct clusters and subclusters, central and laterals dense and thick in fruit, 8–30 mm x 4–6 mm; floral bracts narrowly triangular to lanceolate or ovate-lanceolate, keeled, 2.1–2.8 mm, 1/2–3/4 as long as the calyces, margins eciliate. **Calyces** 3–3.5 mm, purplish, hirsutulous to hirsutulous-hirtellous or hirtellous, stipitate-glandular, lobes connivent. **Corollas** purple to blue-violet or pinkish, tubes 4–6(–7) mm, 1.5–2 mm longer than the calyces, limbs 2–5 mm in diam. **Nutlets** 1.5–1.9 mm, commissural faces extending to very tip of nutlets, densely papillate to papillate-bullate. $2n$ = 12, 14, 28.

Flowering May–Jul(–Sep). Roadsides, fields, clearings, depressions, disturbed sites; 10–100 m; introduced in Ark., Calif., Ga., La., Mass.(?), Miss., Mo., N.Y., N.C., Oreg., S.C., Tenn.(?); native to South America (southern Brazil, Uruguay, Paraguay, northern Argentina); introduced also in Asia (Taiwan fide S. M. Chaw et al. 1986), Africa, Indian Ocean Islands (Mauritius), Pacific Islands (New Zealand), Australia.

Verbena bonariensis is easily recognizable, especially in vivo (fide numerous photos) where the long floral tubes are conspicuous, and even in the herbarium. Upon seeing the prominent flowers, examine the peduncles and calyx with a lens to confirm the presence of glandularity. The difference in leaf morphology also can be confirmed with a small set of specimens—leaves of *V. bonariensis* tend to be narrower than in *V. incompta*. In addition to the distinctions in the key, in *V. bonariensis* the non-glandular hairs are thinner and the plants apparently are generally shorter in stature and more clearly annual in duration. Described differences in shape and size of the inflorescence do not appear

to be consistent, except in the elongation of fruiting spikes. Within each species, South American plants are similar in variability to the North American ones.

Most internet photos of "*Verbena bonariensis*" show the typical form, which is cultivated for its showy, fragrant flowers. Photos of both species, from California plants, are shown on CalPhotos (http://calphotos.berkeley.edu). In the USA, however, the few collections of naturalized plants indicate that typical *V. bonariensis* occurs much less commonly than *V. incompta*.

Moldenke identified typical *Verbena bonariensis* as var. *conglomerata*. He cited (1962a, p. 267) only two collections of var. *conglomerata* from non-cultivated plants growing in the USA: **California**. Sonoma Co., Sebastopol, garden weed, 14 May 1961, *Noldeke s.n.* (LL); **Tennessee**. Knox Co., in the back yard of J.M. Brown, 1601 Lombard Place, probably a hybrid, 29 Jun 1954, *Hoss 18323* (TENN). Otherwise, plants apparently have been so identified in the USA only by Sorrie and Somers (1999), who noted the occurrence of "var. *conglomerata*" in **Massachusetts.** Hampshire Co.

Collections examined. **Arkansas**. Ashley Co.: P.O. Hamburg, damp woods, 250 ft, 11 Jun 1938, *Demaree 18637* (MO). **California**. Los Angeles Co.: San Bernadino Basin, alluvial fan of San Antonio Cayon, along Baseline Blvd, on S side of road between Monte Vista Ave. and Central Ave., presumably a waif, disturbed alluvial soil of parkway between road and old quarry fence, 12 May 2000, *Boyd et al. 10306* (TEX). Sonoma Co.: Sebastopol, garden weed, 14 May 1961, *A.M. Noldeki s.n.* (LL). **Georgia**. Jefferson Co.: Wrens, frequent on sandy loam, 15 Jun 1959, *Kral 9074* (VDB-2 sheets). **Louisiana**. Morehouse Par.: ditch beside Par. Rd. 5802, S of La. 134, 15 Jul 1977, *Thomas 54092* (NLU); weed in cemetery beside La. 834 N of Jones and W of US 165, 25 Jul 1983, *Thomas et al. 84586* (BRIT, NLU-2 sheets); edge of pine woods S of dirt road along Arkansas state line N of La. 834 and W of Jones, 4 Jun 1989, *Thomas 110,732* (BRIT, NLU). Jefferson Davis Par.: roadside ditch, US 90 ca 1 mi E of Jennings, 30 May 1986, *Allen 13120* (NLU). Vernon Par.: ca. 7 mi N of Pitkin, near Cooter's Bog, off La. 467, 19 Jun 2002, Allen 18970 (NLU). **Mississippi**. Hinds Co.: roadbank of Miss. 27 on hilltop W of Bear Creek Road, 10.3 mi NW of I-55 at Crystal Springs, 17 May 1983, *Thomas et al. 83445* (BRIT). Wilkinson Co.: along new gas line ROW in gorges N of Miss. 24, E of Lessley and ca. 10 mi W of Woodville, 17 Jun 1993, *Thomas 140,086* (NLU). **Missouri**. St. Louis Co.: St. Louis, 4500 block of Shaw Avenue, just W of RR crossing on S side of road, area of fill dirt storage, 9 Oct 2002, *Yatskievych et al. 02-77* (MO). **New York**. Bronx Co.: New York Botanical Garden, near Operations where soil and trees dumped, ca. 2 dozen plants on steep bank of gravelly soil, 6 Jul 1997, *Nee 47132* (TEX). **North Carolina**. Bladen Co.: weedy old field, NC Rte 41, 8.5 mi E of White Lake, 2 Jul 1950, *Fox and Boyce 3783* (SMU). Tyrrell Co.: 4 mi W of Columbia, edge of fields, 18 Aug 1957, *Reed 40224* (MO). **Oregon**. Linn Co.: weedy area by the holding ponds behind the OSU Salmon Disease Lab, just E of Corvallis, 61 meters, 9 Sep 2000, *Halse 5935* (BRIT). **South Carolina**. Barnwell Co.: Savannah River Operation Area (A.E.C.), Station 74, swamp flat at end of road, 4 Jun 1969, *Kelley 74* (MO). Charleston Co.: roadside near Charleston, Sep [without year], *Curtis 1963* (MO-2 sheets); Port of Charleston, wastes, 17 May 1979, *Reed 139497* (MO). Edgefield Co.: sandy peaty swale by intersect. US 25 and SC 121, 11 Aug 1995, *Kral 85469* (VDB). Greenville Co.: jct of Standing Spring Rd and Laurens Rd, 16 Jun 1974, *Boufford 14361* (MO). McCormick Co.: field near SC 28, 2 mi S of Plum Branch, 11 May 1957, *Radford 22293* (VDB).

VERBENA INCOMPTA P.W. Michael, Telopea 62: 181. 1995. **TYPE: Australia**. Victoria. Bright-Tawonga Rd. 9.7 km ESE of Bright, ca. 3.2 km E of Tawonga-Harrietville road fork, 25 Mar 1964, *R.V. Smith 64/64* (holotype: MEL; isotype: NSW).

Verbena bonariensis var. *brevibracteata* Kuntze, Rev. Gen. Pl. 3: 254. 1898. *Verbena litoralis* var. *brevibracteata* (Kuntze) O'Leary, Ann. Missouri Bot. Gard. 94: 598. 2007. **LECTOTYPE** (O'Leary 2006, p. 494): **Brazil**. Prov. Tucumán. Sierra de la Cuesta del Garabatal, 30 Jan 1874, *P.G. Lorentz 853* with Hieronymus (NY digital image!; isolectotypes: CORD, SI).

The NY lectotype of *Verbena bonariensis* var. *brevibracteata* clearly shows broadly clasping leaf bases characteristic of *V. bonariensis* and *V. incompta*, rather than, in the concept here, the basally attenuate to short-petiolate bases of *V. brasiliensis* or *V. litoralis*. O'Leary (2006) and O'Leary et al. (2007) studied the isolectotypes at CORD and SI—the illustration of var. *brevibracteata* by O'Leary et al. shows subclasping leaf bases, and their description of var. *brevibracteata* notes leaf bases "subamplexicaul to at times slightly auriculate." In the concept here, however, plants with clasping leaf bases are identified as *V. bonariensis* and *V. incompta*. Var. *brevibracteata* was described by O'Leary et al. as eglandular and is placed here as a synonym of *V. incompta*.

Plants annual or short-lived perennial, taprooted or with ligneous fibrous roots. **Stems** erect, 100–200 cm, scabrous to hispid or hispid-hirsute, eglandular. **Leaves** persistent, ovate to ovate-lanceolate, oblong-elliptic, or obovate, basally subclasping and subcordate, midstem blades (3–)5–10 cm x 10–35 mm, veins impressed adaxially, hispid-hirsute on both surfaces or strigose-hirsute adaxially, margins coarsely serrate; petioles absent. **Spikes** in 3s, forming compound cymes, the central mostly sessile on peduncles 0(–3) mm, inflorescence aspect corymbiform, comprising relatively compact and distinct clusters and subclusters, central and laterals dense and thick in fruit, (6–)10–40(–55) mm x 4–6 mm; floral bracts ovate to lanceolate or narrowly lanceolate, keeled, 3–4 mm, slightly longer than the calyces or equal, margins ciliate. **Calyces** 2.5–3.5 mm, strigose to strigose-hirsute, eglandular, lobes connivent. **Corollas** purple to red-purple, violet, or white, tubes 2.5–4 mm, limbs 3.5–5.5 mm in diam. **Nutlets** 1–1.2 (–1.4) mm, commissural faces extending to very tip of nutlets, densely bullate.

Flowering May–Jul(–Sep). Seasonally wet places, creek sides, mesic disturbed woods, fields, clearing, swales, ditches, borrow pits, disturbed sites; 5–100 m; introduced in Ont., Que.; Ala., Ariz., Ark., Calif., Fla., Ga., Ill., La., Mass., Miss., N.J., N.Y., N.C., Okla., Oreg., S.C., Tenn., Tex., Va.; native to South America; introduced also in Central America, Europe, Asia, Africa, Pacific Islands (Fiji, New Zealand, Norfolk Island, Papua New Guinea), Australia.

Distinction between *Verbena brasiliensis* and *V. litoralis*

The distinction between *Verbena brasiliensis* and *V. litoralis* is problematic, judging from recent literature, although the problem does not exist in North America. Both names have been used for plants identified at specific rank, and infraspecific variants have been named in each. *Verbena brasiliensis* has been treated as a variety of *V. litoralis* by Munir (2002) and O'Leary et al. (2007) because of the existence of putative intermediates. Some plants identified here as *V. incompta* were included by O'Leary et al. within their concept of *V. litoralis* (as var. *brevibracteata* = *V. brasiliensis*). The present commentary perhaps does not settle the matter but hopefully adds useful perspective.

Munir (2002, p. 75) observed that he "found no character(s) to maintain *V.*[*erbena*] *litoralis* and *V. brasiliensis* as distinct species. Both are extremely variable in the shape and size of the leaves, length and diameter of the spikes, [and] congestion and laxity of flowers particularly in the lower part of their spikes. For each character there seem to be intermediates between the two taxa although there are some extreme cases where these taxa look different from each other in the size and shape of their leaves and spikes. Due to the presence of these intermediates, it has been difficult to draw a line between the two." On the other hand (and seemingly in contrast), Munir noted (p. 75) that "var.

brasiliensis may readily be identified …" by the contrasts below, and he mapped var. *litoralis* and var. *brasiliensis* as almost completely sympatric in Australian distribution, without indication of intermediates.

Munir (2002)

1. Spikes dense at first, later elongating with flowers remote in the lower half of the rachis, usually 3–8(–12) cm long; stems 4-angled but not sharply so; hairs on rachis, bracts, and calyx minute and closely appressed; floral bracts ovate to ovate-lanceolate, subequal or somewhat shorter than the calyx; leaf blades attenuate toward the base, margins serrate-dentate, with both blunt (rounded) and sharp teeth ..... **Verbena litoralis** var. **litoralis**

1. Spikes dense, not elongating, (1–)2–6(–8, rarely –15), with closely congested flowers; stems very sharply angled; hairs on rachis, bracts, and calyx spreading; floral bracts narrowly lanceolate, equalling the calyx or slightly longer; leaf blades cuneate toward the base, sometimes half-clasping, margins serrate-dentate ..... **Verbena litoralis** var. **brasiliensis**

O'Leary et al. (2007) followed essentially the concept of Munir (2000) in distinguishing *Verbena litoralis* and *V. brasiliensis* and also in treating them as varieties of a single species (but using "var. *brevibracteata*" as the name for the "brasiliensis" entity). They noted that *V. litoralis* is variable throughout its range but did not comment on biological interaction between the two varieties or on putative intermediacy and intergradation. Typical *V. litoralis* has a considerably wider South American distribution than var. *brevibracteata*, but O'Leary et al. viewed the two entities as sympatric (as interpreted through specimen citations) in parts of Brazil and Paraguay and in all of Argentina except southernmost provinces (Chubut and Santa Cruz).

O'Leary et al. (2007)

1. Leaves basally attenuate-cuneate to subpetiolate, the basal up to 5 cm long and 2.5 cm wide; inflorescence puberulent, eglandular; flowers remote in the basal part of the rachis; floral bracts ovate; corolla tubes 3–4 mm ..... **Verbena litoralis** var. **litoralis**

1. Leaves basally subamplexicaul, exceptionally [or "at times"] auriculate, the basal up to 10 cm long; inflorescence pilose or sometimes strigose, bracts and calyces sometimes with a few glandular hairs; flowers densely imbricate along the rachis; floral bracts narrowly ovate; corolla tubes ca. 4.5 mm ..... **Verbena litoralis** var. **brevibracteata**

Using a contrast in inflorescence architecture, O'Leary et al. (2007, couplet 13a/b, p. 579) distinguished *Verbena bonariensis* (including two varieties) from *V. litoralis* (including var. *brevibracteata* = *V. brasiliensis* and var. *litoralis*).

13a. Florescencias reunidas en paracladios multímeros aglomerados en torno a la florescencia principal, nunca superándola ..... **Verbena bonariensis**

13b. Florescencias reunidas en paracladios trímeros no aglomerados en torno a la florescencia principal, superándola ..... **Verbena litoralis**

An earlier study of inflorescence architecture in *Verbena* (Martínez et al. 1996) underlies the concepts and descriptions used by O'Leary et al. The contrast (as in 13a/b) is freely interpreted here in less technical terms ("paracladia" are branches similar in structure to the florescence of the main axis—in *Verbena* essentially spikes mostly in 3's or groups of spikes in 3's) and somewhat expanded. The difference essentially reflects the degree of foreshortening of peduncles and spikes.

a. Central spikes mostly sessile, with short-pedunculate lateral spikes relatively short in fruit and closely clustered, the whole inflorescence with a corymbiform aspect, comprising relatively compact and distinct clusters and subclusters ..... **Verbena bonariensis**

a. Central spikes relatively long-pedunculate, with long-pedunculate lateral spikes relatively elongate in fruit and loosely associated, the whole inflorescence loosely paniculiform aspect, comprising well-separated spikes ..... **Verbena litoralis**

This contrast is appropriate as a distinction between *V. bonariensis* and *Verbena litoralis*, but as the taxa are understood here, the inflorescence of *V. brasiliensis* is essentially identical to that of *V. bonariensis* and *V. incompta*, not like that of *V. litoralis*. Inflorescence architecture is a conspicuous difference between *V. brasiliensis* and *V. litoralis*, but other features also separate them—*V. brasiliensis* has taller, more hispid, and thicker stems, thicker leaves with veins impressed adaxially, and larger floral bracts, calyces, and corollas.

VERBENA BRASILIENSIS Vell., Fl. Flumin., 17. 1829. *Verbena litoralis* var. *brasiliensis* (Vell.) Briq. [nom. illeg.], Ann. Conserv. Jard. Bot. Genève 7-8: 292. 1904. **TYPE**: **Brazil**. Rio de Janeiro, without data. **LECTOTYPE** (Verdcourt 1992, p. 9): Vellozo, Fl. Flumin., Icon. 1: plate 40. 1831 ("1827").

In proposing the nomenclatural combination, Briquet (1904) intended this variety to characterize the typical expression of the species and explicitly included "*V. litoralis* Kunth, l.c., sensu stricto" as a synonym. O'Leary et al. (2007) correctly that noted that Briquet's combination was invalid and attributed its authorship to Munir (2002), but Munir simply cited the Briquet reference and did not make the combination.

Verbena quadrangularis Vell., Fl. Flumin., 16. 1829 ("1825"). **TYPE**: **Brazil**. Rio de Janeiro, without data. **LECTOTYPE** (Verdcourt 1992, p. 10): Vellozo, Fl. Flumin., Icon. 1: plate 39. 1831 ("1827").

Verbena hansenii Greene, Pittonia 3: 308. 1898. **TYPE**: **USA**. California. Amador Co.: Clinton, foothills of the Sierra Nevada, 1889, *G. Hansen s.n.* (holotype: ND-G; isotypes: K, MO-as cited by Perry 1933). See comments by O'Leary et al. on the disparity between collection data in the protologue and on the presumed ND-G holotype. Identified by O'Leary et al. as the "brasiliensis" expression. A topotype identified by the collector as *Verbena hansenii* is *V. brasiliensis*: California. Amador Co.: Clinton, 2000 ft, 6 Oct 1896, *G. Hansen 2025* (MO!).

Verbena litoralis forma *angustifolia* Chod., Bull. Herb. Boissier, ser. 2(9): 818. 1902. **TYPE**: **Paraguay**. Tucangua, Feb 1897, *E. Hassler 3853* (holotype: BM; isotypes: G, NY-2 sheets digital images!). Leaves are narrow but coarsely serrate; fruiting spikes dense except at the base, where looser and fruits deciduous, central spikes nearly sessile. Identified as *V. brasiliensis* by Moldenke, as *V. litoralis* sensu stricto by O'Leary et al.

Verbena approximata Briq., Ann. Conserv. Jard. Bot. Geneve 7-8: 292. 1904. **TYPE**: **Paraguay**. Grand Chaco, en face de l'Assomption, 1875, *B. Balansa 1027c* (holotype: P; isotypes: G, P, SI). Not seen. Identified by O'Leary et al. (and earlier by Troncoso) as *V. litoralis*. A paratype clearly is *V. brasiliensis*: **Paraguay**. Sierra de Maracayú, vicine Igatimí, Oct, *E. Hassler 4887* (G-Delessert, photo-MO!).

Verbena brasiliensis var. *subglabrata* Moldenke, Phytologia 3: 278. 1950. **TYPE**: **Chile**. [Prov. Colchagua], San Fernando, 7 Feb 1930, *E. Barros V. 8050* (holotype: NY digital image!). The NY sheet bears only a leafless portion of inflorescence, which has dense, short, sessile to subsessile central and lateral spikes. It is apparently out of range for *V. bonariensis* and *V. incompta*.

Verbena chacensis Moldenke, Phytologia 5: 228. 1955. **TYPE**: **Paraguay**. Gran Chaco, Loma Clavel, Nov 1903, *E. Hassler 2459* (holotype: UC, fragment TEX!; isotypes; P, SI). Identified by Munir and O'Leary et al. as the "brasiliensis" expression.

Verbena litoralis Kunth var. *congesta* Moldenke, Phytologia 20: 80. 1970. **TYPE**: **Mexico**. Sinaloa. Mpio. Badiraguato, Sierra Surutato, along a small stream 0.5 of a mile N of Los Ornos, slope with *Quercus urbani*, *Quercus epileuca*, *Pinus lumholzii*, *Pinus ayacahuite*, and *Arbutus xalapensis*, 1 Nov 1969, *D.E. Breedlove & F.S. Kawahara 16735* (holotype: TEX!; isotype: SI). Identified by O'Leary et al. as the "brasiliensis" expression, tentatively confirmed here.

Plants annual or short-lived perennial, taprooted or with ligneous fibrous roots. **Stems** erect, 70–150(–250) cm, sparsely to moderately hispid. **Leaves** persistent, lanceolate to rhombic-lanceolate

or lanceolate-elliptic, cuneate-attenuate at base, midstem blades (2–)5–8 cm x 10–25 mm, veins impressed adaxially, adaxially strigose-hirsute, abaxially hirsute mostly along the veins, margins serrate; petioles absent. **Spikes** in 3s, forming compound cymes, the central sessile to subsessile on peduncles 0–5(–10) mm, inflorescence aspect corymbiform, comprising relatively compact and distinct clusters and subclusters, central and laterals dense and thick in fruit, (5–)10–30(–50) mm x 3–5 mm; floral bracts narrowly lanceolate, 2.5–4 mm, about equal or longer than the calyces. **Calyces** (2.5–)3–3.5 mm, loosely strigose to hirsute-strigose, eglandular, lobes connivent. **Corollas** usually purple to blue or blue-violet, tubes 3–4 mm, limbs (2–)2.5–3.5 mm in diam. **Nutlets** 1–1.4 mm, commissural faces extending to very tip of nutlets, densely papillate. $2n = 28$.

Flowering (Apr–)May–Sep. Cut-over pine and oak-pine woods, pine flatwoods, river bottoms, river and canal banks, marsh edges, creek bottoms, hillside seeps, ditches, depressions, shell banks, clearings, vacant lots, fields and pastures, roadsides, fence rows, disturbed sites; 10–100(–200) m; introduced in Ala., Ark., Calif., Fla., Ga., Ky., La., Miss., Mo., N.C., Okla., Oreg., S.C., Tenn., Tex. Va.; native to South America; introduced also in Mexico (Michoacan, Nuevo León, Sinaloa), Europe, Africa (South Africa), Madagascar, Australia.

Suksdorf 1980 was cited by Moldenke (1962b) as *Verbena brasiliensis* and its identity is confirmed here. **Oregon**. [Multnomah Co.]: Linnton near Portland, 11 Aug 1914, *Suksdorf 1980* (WS digital image!).

If *Verbena brasiliensis* is treated at varietal rank within *V. litoralis*, the earliest available name at that rank is *V. brasiliensis* var. *subglabrata*, which would have to be transferred to *V. litoralis*. The name used by Munir (2002), *V. litoralis* var. *brasiliensis*, is illegitimate. The clasping leaves and eglandular vestiture of the type of *V. litoralis* var. *brevibracteata* place this taxon as a synonym of *V. incompta*, the small-flowered, eglandular expression of *V. bonariensis* sensu lato (see comments above). In the present perspective, *V. brasiliensis* and *V. litoralis* are distinct species.

Verbena brasiliensis and *V. quadrangularis* are from the same publication by Velloso—Yeo (1990) considered them to synonymous, noting that Velloso described *V. brasiliensis* as differing only in having a 4-lobed corolla (vs. 5-lobed in *V. quadrangularis*), one lobe being larger than the others and crenate, and apparently in producing two nutlets per fruit instead of four. Michael (1997) noted that such corolla morphology occurs in sterile plants that apparently are hybrid between *V. litoralis* and fertile *V. brasiliensis*-like plants. He identified the latter as *V. quadrangularis*, the sterile hybrids as as *V.* ×*brasiliensis*. O'Leary et al. (2007) studied "numerous specimens" of *V. brasiliensis* (as "*V. litoralis* var. *brevibracteata*") and found none with aberrant features. Since the putative hybrid shows no other morphological features suggestive of hybridization with *V. litoralis*, *V. brasiliensis* is maintained here as the name of this widespread adventive.

Status of *Verbena sphaerocarpa*.

Verbena sphaerocarpa was treated by O'Leary et al (2007) as a synonym of *V. litoralis*. These plants, however, have the habit, inflorescence, and stem and leaf vestiture of *V. brasiliensis*, but the leaves are oblong-elliptic, entire to subentire, and petiolate, and as noted by Perry (p. 256), "the schizocarp is fully as broad as or even broader than long, an unusual trait not found elsewhere in the North American species of *Verbena*." Calyces of *V. sphaerocarpa* are 2–2.3 mm (vs. (2.5–)3–3.5 mm in *V. brasiliensis*) and floral bracts are ovate-triangular and 1/2–2/3 the calyx length (vs. narrowly lanceolate and equal or longer than the calyx). Limited evidence suggests these plants are justifiably recognized as distinct.

Verbena sphaerocarpa Perry, Ann. Missouri Bot. Gard. 20: 256. 1933. **TYPE**: **Mexico**. Colima. Socorro Island, Mar-Jun 1897, *A.W. Anthony 380* (holotype: MO digital image!; isotypes: GH, US digital image!).

Additional collections examined: Socorro Island: Evermann Peak, slopes of volcanic cone within 50 m of summit, 1000+ m, 21 Mar 1967, *Felger 15758* (ARIZ); south slope of Mt. Evermann, 600 m, 20 Mar 1967, *Felger 15822* (ARIZ); Grayson's Cove, 4 May 1925, *Mason 1612* (MO!).

VERBENA LITORALIS Kunth in Humboldt et al., Nov. Gen. Sp. 2(qto.): 276, plate 137. 1818. **LECTOTYPE** (Macbride 1960, p. 624): **[Peru]**. Trujillo, *A. Bonpland s.n.* (P; isotype: SI). Plate 137 nicely illustrates the open inflorescence of slender, long-pedunculate spikes with fruits becoming remote proximally as they mature.

In comments on *Verbena bonariensis*, Hooker (Bot. Misc.1: 166. 1829) said "The *Verbena littoralis* of Humboldt seems to be a variety of this with shorter spikes than usual." This statement sometimes has been taken as validation of the combination "*V. bonariensis* var. *litoralis* (Kunth) Hook.," but it was inadequate for validation since the publishing author must definitely associate the epithet with the name of the genus (ICBN Art. 33.1).

Verbena caracasana Kunth, Nov. Gen. Sp. 2(qto.): 275. 1818. *Verbena litoralis* var. *caracasana* (Kunth) Briq. [nom. illeg.], Ann. Conserv. Jard. Bot. Genève 7-8: 292. 1904. **LECTOTYPE** (O'Leary 2006, p. 494): **Venezuela**. "Rarissime in sylvaticis prope Caracas," *F.W. Humboldt and A. Bonpland 658* (P fiche!; isolectotypes: B photo MO!, SI).

Briquet explicitly intended the combination "var. *caracasana*" as a replacement name for *V. litoralis* var. *leptostachya* Schauer.

Verbena affinis Mart. & Gal., Bull. Acad. Roy. Sci. Bruxelles 11: 322. 1844. **TYPE**: **Mexico**. Michoacan. Morelia, 1956 m, 1840, *H.G. Galeotti 781* (holotype: BR photo-TEX!; isotype: BR, K photo-MO!). Identified as *V. litoralis sensu stricto* by O'Leary et al. (2007).

Verbena longifolia Mart. & Gal., Bull. Acad. Roy. Sci. Bruxelles 11: 323. 1844. **TYPE**: **México**. Michoacan. [Mpio. Ario], dans les champs d'Ario [de Rosales], 4000 ft, Aout 1840, *H. Galeotti 791* (holotype: BR, photos at LL!, also F, NY, SI, and Z, fide Moldenke 1964b). The protologue noted glabrous stems and glabrous, filiform, elongate spikes in a panicle, specifically comparing it to *V. urticifolia*. O'Leary et al. (2010) place *V. longifolia* as a synonym of *V. carolina* L.

Verbena litoralis var. *leptostachya* Schauer in A. D.C., Prodr. 11: 542. 1847. **LECTOTYPE** (Munir 2002, p. 65): **Mexico**. [Veracruz]. Ad Jalapam et Papantlam, *C.J.W. Schiede 1168* (HAL). Placed as a synonym of *V. litoralis* by O'Leary et al (2007).

Verbena litoralis var. *pycnostachya* Schauer in A. D.C., Prodr. 11: 542. 1847 [nom. illeg.]. Schauer cited *V. litoralis* in synonymy, as well as *V. brasiliensis*.

Verbena litoralis var. *glabrior* Bentham, Bot. Voy. Sulphur, 153. 1846. **TYPE**: **Peru**. [Prov. Paita]: "Peita" [Paita], no other data (holotype: K?). Not seen. Protologue: "706. VERBENA *littoralis*, var.? glabrior, foliis hinc inde trifidis grosse et obtusiuscule inciso-dentatis. An species propria? Folia *V. menthaefoliae*, Benth. Pl. Hartw. p. 21. sed flores parvi V. littoralis.—Peita."

Verbena nudiflora Nutt. ex Turcz., Bull. Soc. Imp. Naturalistes Moscou 36(2): 195. 1863. **TYPE**: **Sandwich Isles** [Hawaii]. "Wahoo" [Oahu], 1835, *T. Nuttall s.n.* (holotype: BM; isotype: PH fide Moldenke 1964b, p. 58). Photos labeled as the BM type of "*Verbena nudiflora*" have been distributed (MO!, SMU!), but the plant pictured is *Allexis cauliflora* Pierre (Violaceae) from tropical Africa, evidently from a labeling error. Munir (2002) cited collections by Funk (*54, 325*) and Galeotti (*359*)—these are paratypes. See further notes by O'Leary (2006).

Verbena paucifolia Turcz., Bull. Soc. Imp. Naturalistes Moscou 36(2): 196. 1863 (non Mart. & Gal. 1844). **TYPE**: **Mexico**. Oaxaca. Without other data, *Botteri 659* (holotype: P?). Attribution of this collection to "*Botteri s.n.*, Texas" by O'Leary et al. (2007) was incorrect. Placed as a synonym of *V. litoralis* fide O'Leary et al.

Verbena integrifolia Sessé & Mociño [nom. illeg.?], Naturaleza (Mexico City), ser. 2, 1: app. 6. 1887 (non Michx. ex Walp., Repert. Bot. Syst. 4: 18. 1845, nom. illeg., in syn.). **TYPE**: **Mexico**.

[Querétaro]. "Habitat in Queretari circuitibus." McVaugh (2000) noted that no corresponding specimen is found in the Sessé & Mociño herbarium. According to Moldenke (1964c, p. 373), "The *V. integrifolia* of Michaux is a synonym of *V. simplex* and was published by Walpers … in synonymy only, so therefore does not invalidate the use of the same epithet by Sessé & Mociño."

Verbena litoralis var. *albiflora* Moldenke, Phytologia 1: 432. 1940. **TYPE**: **Mexico**. Michoacan. Distr. Coalcoman, Coalcoman, llano, 1000 m, 20 Jul 1939, *G.B. Hinton 13965* (holotype: LA photo-LL!; isotype: US digital image!).

Verbena gentryi Moldenke, Phytologia 2: 27. 1941. **TYPE**: **Mexico**. Sinaloa. Sierra Monterey, Quebrada de Platano, moist canyon bottom, short tree forest, 1500 ft, 13 Mar 1940. *H.S. Gentry 5923* (holotype: NY digital image!; isotypes: F digital image!, MICH digital image!). O'Leary et al. (2010) place *V. gentryi* as a synonym of *V. carolina* L.

Verbena longifolia forma *albiflora* Moldenke, Phytologia 7: 430. 1961. **TYPE**: **México**. Oaxaca. Vicinity of Cerro Zempoaltepetl, E slopes near Patio de Arena ca. 5 km E of summit, cloud forest, along moist claybanks drainage area from cornfield cleared among *Persea*, ca. 2900 m, 7 Aug 1950, *B. Hallberg 813* (holotype: MICH digital image!; isotypes: DS, LL! digital image!, US digital image!). O'Leary et al. (2010) place this as a synonym of *V. carolina* L.

Verbena longifolia var. *pubescens* Moldenke, Phytologia 13: 307. 1966. **TYPE**: **México**. Oaxaca. 19 km SW of Sola de Vega along road to Puerto Escondido, steep slope with *Quercus* and *Pinus*, 7000 ft, 30 Aug 1965, *D.E. Breedlove 12292* (holotype: LL! digital image!; isotypes: DS, MICH digital image!). O'Leary et al. (2010) place this as a synonym of *V. carolina* L.

Verbena integrifolia Sessé & Mociño forma *albiflora* Moldenke, Phytologia 16: 95. 1968. **TYPE**: **Mexico**. Michoacan. 18 mi E of Zamora, 20 Jun 1967, *A.R. Moldenke 1750* (holotype: TEX! digital image!; isotypes: TEX!, SI).

Verbena minutiflora Briq. ex Moldenke var. *peruviana* Moldenke, Phytologia 50: 14. 1981. **TYPE**: **Peru**. Prov. Cajamarca. Pampa de la Culebra (Cajamarca-La Encañada), terreno cultivado, 2900 m, 18 May 1976, *A.J. Sagastegui et al. 8385* (holotype: TEX! digital image!; isotypes: MO! digital image!, SI). Plants depauperate and deformed, spikes short and atypical. Identified by O'Leary et al. (2007) as *V. montevidensis*.

Verbena litoralis var. *portoricensis* Moldenke, Phytologia 50: 310. 1982. **TYPE**: **Puerto Rico**. Cayey. On Panoramic Highway, south of Cayey, 640 m, 14 Mar 1979, *A.H. Liogier 28417* (holotype: NY digital image!). Identified by Munir and O'Leary et al. as *V. litoralis* sensu stricto, tentatively corroborated here, although the large cauline leaves are unusual.

Plants annual or short-lived perennial, taprooted or fibrous rooted. **Stems** erect, 50–100 cm, sparsely strigose to hirsute-strigose or hispid-hirsute, eglandular. **Leaves** persistent, lanceolate to elliptic-lanceolate or oblanceolate, midstem blades 2–5(–11) cm x 1–1.5 cm, veins not impressed adaxially, hirsute-strigose adaxially, glabrate to sparsely or moderately strigose-hirsute abaxially, eglandular, margins coarsely serrate on distal 1/2–2/3, not revolute; petioles absent or 1–5 mm. **Spikes** in 3s, forming obscure compound cymes, central pedunculate on peduncles 10–40 mm, inflorescence aspect loosely paniculiform, comprising well-separated spikes, central and laterals, 3–15 cm x 2–3 mm, fruits becoming remote on at least the proximal 1/4–1/2; floral bracts ovate-lanceolate, 1–1.5 mm, shorter than the calyces, margins ciliate, adaxial surface glabrous to sparsely strigose. **Calyces** 1.8–2.2 mm, sparsely and loosely strigillose to hispidulous-strigose, eglandular, lobes connivent. **Corollas** white to blue, purplish, or pale violet, tubes 2–2.5(–3) mm, 0–0.5(–1) mm longer than the calyx, limbs 1.5–2 mm in diam. **Nutlets** 1.1–1.5 mm, commissural faces extending to very tip of nutlets, bullate, rarely bare. $2n = 28$.

Flowering Feb–Oct. Openings, disturbed sites; 600–2700 m; not known in the USA; native to northern and western South America (northwestern Argentina, Bolivia, Chile, Columbia, Ecuador, Peru, Venezuela), northward through Central America and Mexico (Aguascalientes, Distrito Federal, Hidalgo, Jalisco, Edo. Mexico, Michoacan, Nuevo León, Oaxaca, Sinaloa, Tabasco, Tamaulipas,

Veracruz); introduced in West Indies, Africa, Indian Ocean Islands (Reunion, Mauritius), Pacific Islands, Australia.

Records previously identified as *Verbena litoralis* from Arkansas, Florida, Oregon, and Texas are identified here as *V. montevidensis* (see below). *Verbena litoralis* also has been cited from other states in the USA, based on concepts that included *V. brasiliensis*. Collections identified as *V. litoralis* from eastern Argentina and Uruguay probably are *V. montevidensis*, as interpreted here.

Plants of *Verbena litoralis* sensu lato in southwestern Mexico (Querétaro, Michoacan, Jalisco, Nayarit, Colima, Sinaloa) commonly have glabrous to glabrate, narrowly oblong narrowly lanceolate-oblong leaves with entire to subentire margins. Similar forms of *V. litoralis* also appear sporadically elsewhere. These have sometimes been identified as *V. integrifolia* Sesse & Moc. and at least at one locality are reported to be hexaploid ($2n = 42$; Lewis & Oliver 1961). Other names applied to this expression are *V. affinis*, *V. litoralis* var. *albiflora*, and *Verbena integrifolia* forma *albiflora*.

Verbena longifolia is included here in synonymy of *V. litoralis*. Perry (1933, p. 272) noted that the latter is "A rather singular species combining the foliar characters of *V. litoralis* with the inflorescence characters of *V. carolina*." Nash and Nee (1984) distinguished the two taxa by the following contrasts (translated from Spanish).

1. Leaf margins serrate above the middle; floral bracts almost two-thirds as long as the calyces; nutlets with muriculate commissural faces ..... **Verbena litoralis**
1. Leaf margins serrate below the middle; floral bracts about as long as the calyces; nutlets with smooth commissural faces ..... **Verbena longifolia**

A review in the present study of several hundred collections of *V. litoralis* and *V. longifolia*-like specimens from MO and TEX-LL shows that there is no unarbitrary distinction. Almost all plants of *V. litoralis* have consistently cymose branching but rarely (Guanajuato, Guerrero, Querétaro) the branches are not opposite and the inflorescence then is similar to the paniculate structure in North American groups. Spikes of some plants have fruits that become remote over the whole length. These variants are similar in every other detail to *V. litoralis* in its common expression throughout Mexico.

Moldenke (1964b) cited collections of *Verbena longifolia* from over a wide range—Coahuila, Jalisco, Michoacan, Morelos, Nayarit, Oaxaca, Puebla, Sinaloa, Sonora, Veracruz. Perry (1933) and Nash & Nee (1984) cited only from Morelos, Oaxaca, Puebla, and Veracruz.

***Verbena montevidensis* in the USA**

Verbena montevidensis has been collected repeatedly in southeastern Arkansas since the mid 1930's—it also probably has been established in Louisiana at least that long—and it also is known from other localities mostly in the southeastern USA. *Verbena montevidensis* is most closely similar to *V. litoralis*, differing from it in its more highly branched inflorescences with shorter and more numerous spikes, central spikes on relatively shorter peduncles, inflorescence more densely corymbiform in aspect, and stems more slender. Leaves of *V. montevidensis* often are deciduous by flowering and vestiture is reduced, with stems usually glabrous to glabrate or sparsely hirsutulous-strigose. O'Leary et al. (2007) distinguished *V. montevidensis* (from *V. litoralis*) by its filiform stems and peduncles, stem height up to 1 meter, and fruiting spikes up to 6 cm long (vs. aspect not gracile, stem height up to 3 m, and fruiting spikes up to 18 cm). In South America, *V. montevidensis* generally is a species of eastern regions, while *V. litoralis* is more montane and mostly in the west.

VERBENA MONTEVIDENSIS Spreng., Syst. Veg. 2 (ed. 16): 747. 1825. **TYPE**: **Uruguay**. Monte Video, *F. Sellow s.n.* (holotype: B[destroyed], photo-LL! photo-MO!).

Verbena parviflora Larranaga, Escritos 2: 9. 1922 (non Ruiz & Pavón 1845). **TYPE**: **Uruguay**. Not seen. Probably *V. montevidensis*, based on provenance and the allusion to small flowers.

Verbena cordobensis Briq., Annuaire Conserv. Jard. Bot. Genève 10: 100. 1907. **TYPE**: **Argentina**. Estancia Germanica pr. Cordoba, Jun-Dec 1874, *P.G. Lorentz 131* (holotype: G?; isotype: M photo-MO!).

Verbena minutiflora Briq. ex Moldenke, Phytologia 7: 84. 1959. **TYPE**: **Uruguay**. Montevideo, *Captain P. King 78* (holotype: G, photo-F!). "This species is related to *V. montevidensis* Spreng., but is easily distinguished in any series of specimens" (from the protologue). Placed as a synonym of *V. montevidensis* fide O'Leary et al. (2007), tentatively corroborated here.

Plants annual, taprooted or fibrous rooted. **Stems** erect, 40–80 cm, glabrous to glabrate or sparsely hirsutulous-strigose. **Leaves** mostly deciduous by flowering, elliptic to narrowly elliptic or lanceolate, basally acute-cuneate, midstem blades 2–4(–5) cm x 4–8 mm, veins impressed adaxially, margins subentire to inconspicuously dentate to shallowly serrate on the distal 1/3–1/2, glabrate or sometimes hirsutulous abaxially along the veins; petioles absent. **Spikes** in 3s, forming compound cymes, central short-pedunculate on peduncles (0–)2–10(–20) mm, inflorescence aspect loosely corymbiform, comprising loosely but distinctly associated spikes, central and laterals (5–)10–35(–50) mm x 2–3 mm in fruit, fruits becoming remote on the proximal 1/4–1/3; floral bracts ovate, 1–2.2 mm, shorter than the calyces. **Calyces** 2–2.5 mm, strigillose, eglandular, lobes connivent. **Corollas** purple to light lavender or white, tubes 2.5–5 mm, 0–0.5 mm longer than the calyx, limbs 1–1.6 mm in diam. **Nutlets** 1.2–1.5 mm, commissural faces extending to very tip of nutlets, minutely bullate-papillate. $2n = 21$.

Flowering Jun–Jul(–Sep). Creek and lake edges, river bottoms, ditches, low woods, fields, roadsides; 10–100 m; introduced in Ala., Ark., Fla., Ga., La., Oreg. (apparently waifs), Tex.; native to South America (Argentina, Brazil, Paraguay, Uruguay).

Representative collections examined. **Alabama**. Montgomery Co.: near Montgomery on I-85, ca. 1 mi E of intersection with US 180, 8 Jul 1969, *Thomas 2300* (BRIT). **Arkansas**. Ashley Co.: Portland, margins of Wells Lake, open ground, 16 Oct 1937, *Demaree 44270* (MO); Portland, around Wells Lake, 115 ft, 16 Oct 1938, *Demaree 16511* (MO, SMU), *17623* (SMU), and *17624* (MO); Hamburg, low areas, 170 ft, 26 Aug 1942, *Demaree 23893* (SMU); Mist, sandy areas, 190 ft, 8 May 1943, *Demaree 24403* (SMU); P.O. Parkdale, Coastal Plain, waste areas, 112 ft, 12 Sep 1973, *Demaree 67598* (MO); wet area and small pond ca. 1 mi W of Sardis Baptist Church between Fountain Hill and Boydell, 12 Jun 1985, *Thomas 92653* (MO); ca. 6 mi W of US 165 and Boydell, field on top of first hill W of flat delta, 20 Jun 1986, *Thomas 97103* (VDB), *Thomas 97104* (NLU). Bradley Co.: Banks, creek banks, 200 ft, 4 Jul 1939, *Demaree 19543* (SMU). Calhoun Co.: Calion, Ouachita River bottoms, road fill, 27 May 1954, *Holberg 475* (SMU). Chicot Co.: Wilmot, valley land, 19 Jul 1946, *Demaree 25674* (SMU). Drew Co.: Monticello, low ridges, 250 ft, 14 Sep 1943, *Demaree 34649* (SMU) and 24649 (VDB). **Florida**. Dade Co.: The Frog Pond, edge of farm field, just W of C-111 Canal, ca. 1.2 mi N of SR 9336, 8 Nov 1997, *Bradley 1191* (FTG digital image!). Walton Co.: savanna along Rte. 20, ca. 6 mi W of Freeport, 3 May 1982, *Correll 53910* (FTG digital image!). Unspecified Co.: south Florida, roadside marl, 29 Jul 1969, *Byrd s.n.* (FTG-2 sheets digital images!). **Louisiana**. Allen Par.: beside US 190 at La 383 E of Kinder, 14 Dec 1982, *Thomas 82761* (LL). Avoyelles Par.: 1/2 mi W of Evergreen, sandy soil of newly planted cane field, Pierce-Kavanaugh refinery, 21 Apr 1957, *Ewan 19083* (LL); Bunkie, May 1931, *Small s.n.* (LL-3 sheets). Caldwell Par.: beside RR tracks and US 165 N of Riverton and S of La. 847, 10 Jul 1987, *Thomas 100,744* (BRIT). Catahoula Par.: 1.7 mi N of Sicily Island, roadside, 19 Sep 1956, *Shinners 24687* (SMU). Bienville Par.: roadbank of I-20 ca. 0.6 mi W of La. 154 (Gibsland exit), W of Arcadia, 11 Jun 1987, *Thomas 100,092* (MO). Evangeline Par.: 7.3 mi N of Turkey Creek, road fill, 5 Oct 1956, *Shinners 24951* (SMU). Franklin Par.: 4.7 mi NNE of Winnsboro, roadside ditch, 19 Sep 1956,

Shinners 24668 (SMU); 6 mi NE of Gilbert, 0.5 mi S of intersection La. 4 and La. 128 on La. 572, cutover hardwoods, 6 May 1981, *Thomas 76152* (BRIT). Jefferson Par.: ca. 3.7 mi W of Lapalco Blvd. near Westwego, cleared recently disturbed area N of US 90, 15 Jun 1981, *Thomas 123,862* (MO). Lincoln Par.: beside I-20 at Rest Area E of La. 145 and Choudrant exit, W of Calhoun, 11 Oct 1986, *Thomas 98774* (MO). Natchitoches Par.: Kisatchie Natl. Forest, moist area beside La. 118 W of La. 117 and E of Little Kisatchie Bayou E of Mink, 9 Jul 1988, *Thomas 105,666* (MO). Ouachita Par.: waste area beside la 553 at Commercial Solvents Storage Area SW of Sterlington, 19 Jul 1983, *Thomas 84556* (LL). Richland Par.: 8.5 mi W of Rayville, silty ditch bank, 27 Jul 1950, *Shinners 12618* (SMU). Sabine Par.: abundant along roadside of La. 473 along Bayou Toro, ca. 2.8 mi NE of Toro, pine-hardwood forest, 24 Jun 1979, *Allen 9131* (BRIT, VDB). St. John the Baptist Par.: W banks of the Mississippi River, fallow fields along River Road (La 18) between Wallace and Johnston, 26 Jul 1981, *Pruski et al. 2133* (TEX). Union Par.: beside Bayou de Loutre and La. 33, S of Marion, 10 Jun 1983, *Thomas 84050* (BRIT). Washington Par.: just E of intersection near Miss. line W of Warnerton, along road at pasture feeding area, 14 Jun 1983, *Thomas 84169* (LL). **Oregon**. [Multnomah Co.]: Albina, Portland, 25 Oct 1900, *Suksdorf 2912* (WS digital image!) and *2913* (WS digital image!). **Texas**. Brazoria Co.: between Navarre Hillhouse Rd. and Stringer Rd., S of County Rd 91, near (S of) FM 518 and W of Old Chocolate Bayou Rd., 30 Apr 1985, *Cowan 5316* (TEX). Liberty Co.: W side of Cleveland, bottoms of East San Jacinto River, by hwy bridge, 13 Aug 1956, *Shinners 24414* (SMU). Limestone Co.: Fort Parker State Park, Hwy 14 and Park Rd 28, Jun 1993, disturbed area, *Singhurst et al. 1748* (BRIT). Newton Co.: 23 Jul 1939, *Tharp s.n.* (TEX). Orange Co.: 6 mi N of Orange, shallow roadside ditch bank, 17 May 1966, *Shinners 31381* (SMU).

Moldenke (1964b, p. 67) cited many of these collections as *Verbena litoralis* (e.g., *Demaree 16511*, *17624*, *19543*, *23893*, *24403*, *24649*, *25674*, *34649*). For *V. montevidensis* in North America, he cited (1964c, p. 161) only collections of Ewan from Louisiana (Avoyelles Par., Evangeline Par.), none from Mexico or the West Indies. Perry cited as *V. litoralis* an additional collection from Lousiana (Terrebonne Par., *Wurzlow s.n.*, NY), which probably is *V. montevidensis*; From California, she included *V. hanseni* as a synonym of *V. litoralis*, but that is identified here as *V. brasiliensis*; other attributions of *V. litoralis* to California also are based on *V. brasiliensis*. The collections from Oregon probably were of waifs, as the species has not subsequently been reported from there. Reports of *V. litoralis* from Georgia (Jones & Coile 1988) probably are based on *V. montevidensis*.

Verbena montevidensis is abundant and widespread in Louisiana. At NLU, I examined collections of the species from these parishes: Allen, Assumption, Beauregard, Bienville, Bossier, Calcasieu, Caldwell, Cameron, Concordia, East Baton Rouge, Evangeline, Franklin, Grant, Iberia, Jackson, Jefferson, LaFourche, LaSalle, Lincoln, Livingston, Madison, Morehouse, Natchitoches, Ouachita, Pointe Coupée, Rapides, Richland, Sabine, St. John the Baptist, St. Landry, St. Mary, Tangipahoa, Tensas, Terrebonne, Union, Webster, and West Carroll. It is likely that the species occurs at least in Mississippi and perhaps more commonly in Alabama and Florida than represented here.

I have seen only a single collection of *Verbena montevidensis* from Mexico: Baja California Sur. Santa Rita, Km 157 Carr. La Paz-Cd. Constitución, arroyo, matorral sarcocaule, 100 m, 11 Jun 1993, *Domínguez 1136* (ARIZ). *Verbena litoralis* is common in Central America, but I have encountered only two collections from there that can be identified as *V. montevidensis*: **Costa Rica**. Prov. San José. San José, open vacant lots, 1160 m, 18 Mar 1965, *Godfrey 67100* (MO). **Nicaragua**. Dept. Managua. Carr. a Las Nubes, a mano izquierdo en un cafetal, 11 Jul 1982, *Mendez R. 9* (MO). It is possible that they are variants of *V. litoralis* but plants of both collections have short spikes clustered on numerous distal branches forming distinctly corymbiform inflorescences.

The following contrasts separate *Verbena montevidensis* and *V. brasiliensis* in the USA, where they occur together.

1. Central spikes pedunculate; proximal portions of stems 2–3 mm in diam., glabrous; inflorescence branches glabrous or proximally very sparsely hirsutulous-strigose; calyces 2–2.5 mm, closely strigillose; corolla limbs 1–1.6 mm in diam. ..... **Verbena montevidensis**
1. Central spikes sessile to subsessile; proximal portions of stems (2.5–)2.8–5 mm in diam. sparsely hirsute to hispid or scabrous at least on the angles; inflorescence branches hirsute to strigose-hirsute or hirsutulous; calyces 3–3.5 mm, loosely strigose to hirsute-strigose; corolla limbs (2–)2.5–3.5 mm in diam. ..... **Verbena brasiliensis**

The collection cited above from Sabine Parish, Louisiana (*Allen 9131*), and from Texas localities have gracile stems, pedunculate central spikes, and small flowers with strigillose calyces, but the inflorescence axes are sparsely hirsutulous-strigillose, slightly atypical for *Verbena montevidensis* elsewhere. Occasional plants of *V. montevidensis* where fruiting spikes remain relatively dense may have an aspect of *V. brasiliensis*, but the inflorescence structure, flower size, and vestiture distinguish them.

Key to the species

The five species discussed in the present study can be distinguished by the contrasts here. All but *Verbena litoralis* are recognized to occur in the USA. *Verbena sphaerocarpa* is contrasted with *V. brasiliensis* in the text above.

1. Leaves basally clasping to subclasping.

    2. Corolla tubes 4–6(–7) mm, 1.5–2 mm longer than the calyces; distal stems, peduncles, and calyces stipitate-glandular; spikes 8–30 mm in fruit; floral bracts 2.1–2.8 mm; nutlets 1.5–1.9 mm; basal and midstem leaves oblong-lanceolate to oblong-oblanceolate ..... **Verbena bonariensis**
    2. Corolla tubes 2.5–4 mm, 0–0.5 mm longer than the calyces; stems, peduncles, and calyces eglandular; spikes 6–55 mm in fruit; floral bracts 3–4 mm; nutlets 1–1.2 (–1.4) mm; basal and midstem leaves ovate to ovate-lanceolate, oblong-elliptic, or obovate ..... **Verbena incompta**

1. Leaves basally attenuate to short-petiolate.

    3. Central spikes sessile to subsessile, spikes compact, 3–5 mm wide, fruits remaining densely overlapping at maturity ..... **Verbena brasiliensis**
    3. Central spikes pedunculate, spikes loose, 2–3 mm wide, with fruits usually becoming remote at least in the proximal portion at maturity.

        4. Fruiting spikes (5–)10–35(–50) mm in fruit, central spikes on peduncles (0–)2–10(–20) mm; inflorescence distinctly corymboid; leaves commonly deciduous by flowering; stems glabrous to glabrate or proximally very sparsely hirsutulous-strigose ..... **Verbena montevidensis**
        4. Fruiting spikes 30–150 mm in fruit, central spikes on peduncles 10–40 mm; inflorescence open and loosely paniculate; leaves persistent at flowering; stems sparsely strigose to hirsute-strigose or hispid-hirsute ..... **Verbena litoralis**

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